***Pre-Darwinian Theories***

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|   | painting of Carolus Linnaeus |
|   | Carolus Linnaeus1707-1778 |

The leading biological scientist of the mid 18th century was the Swedish botanist Karl von Linné (**Carolus Linnaeus** in Latin).  His 180 books are filled with precise descriptions of nature, but he did little analysis or interpretation. This is to be expected since Linnaeus apparently believed that he was just revealing the unchanging order of life created by God.  The goal of documenting change in nature would not have made sense to him.  Late in his life, however, he was troubled by the fact that plant hybrids could be created by cross pollination.  These were varieties that had not existed before.  Linnaeus stopped short of concluding that these plants had evolved.

Despite his limiting research bias, Linnaeus was a first class scientist.  His most important contribution to science was his logical classification system for all living things which he proposed in his book *Systema Naturae*, first published in 1735.  In this and subsequent works, he described plants and animals on the basis of physical appearance and method of reproduction.  He classified them relative to each other according to the degree of their similarities.  He used a binomial nomenclature in naming them.  That is to say, organisms were given two Latin names--genus and species.  Each genus could have many related species.  Each genus was also part of larger categories of living things.  This Linnaean system of classification is today the basis for naming and describing organisms in all fields of biology.

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| http://anthro.palomar.edu/evolve/images/John_Ray.jpg |
| John Ray1627-1705 |

The concept of genus and species was actually developed in the late 1600's by **John Ray**, an English naturalist and ordained minister.  However, it was Linnaeus who used this system to name us *Homo sapiens* (literally, "wise men").  He also placed us in the order *Primates* (a larger, more inclusive category than our genus) along with all of the apes, monkeys, and prosimians.  This was very controversial at the time since it implied that people were part of nature, along with other animals and plants.  In addition, it meant that we were biologically closer to the other primates than to all other animals.

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|   | painting of the Comte de Buffon |
|   | Comte de Buffon1707-1788 |

Late in the 18th century, a small number of European scientists began to quietly suggest that life forms are not fixed.  The wealthy French mathematician and naturalist, George Louis Leclerc, Comte de **Buffon** , actually said that living things do change through time.  He speculated that this was somehow a result of influences from the environment or even chance.  He believed that the earth must be much older than 6000 years.  In 1774, in fact, he speculated that the earth must be at least 75,000 years old.  He also suggested that humans and apes are related.  Buffon was careful to hide his radical views in a limited edition 44 volume natural history book series called *Histoire Naturelle* (1749-1804).  By doing this, he avoided broad public criticism.

Buffon was an early advocate of the Linnaean classification system.  He was also a quiet pioneer in asserting that species can change over generations.  However, he publicly rejected the idea that species could evolve into other species.  One of his most significant contributions to the biological sciences was his insistence that natural phenomena must be explained by natural laws rather than theological doctrine.

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| painting of Erasmus Darwin |
| Erasmus Darwin1731-1802 |

Another late 18th century closet-evolutionist was **Erasmus Darwin** , the grandfather of the well known 19th century naturalist, Charles Darwin.  Erasmus was an English country physician, poet, and amateur scientist.  He believed that evolution has occurred in living things, including humans, but he only had rather fuzzy ideas about what might be responsible for this change.  He wrote of his ideas about evolution in poems and a relatively obscure two volume scientific publication entitled *Zoonomia; or, the Laws of Organic Life* (1794-1796).  In this latter work, he also suggested that the earth and life on it must have been evolving for "millions of ages before the commencement of the history of mankind."

The first evolutionist who confidently and very publicly stated his ideas about the processes leading to biological change was a French protégé of the Comte de Buffon.   He was Jean-Baptiste Chevalier de **Lamarck**.  Unfortunately, his theory about these processes was incorrect.

Lamarck believed that microscopic organisms appear spontaneously from inanimate materials and then transmute, or evolve, gradually and progressively into more complex forms through a constant striving for perfection.  The ultimate product of this goal-oriented evolution was thought by Lamarck to be humans.  He believed that evolution was mostly due to the **inheritance of acquired characteristics** as creatures adapted to their environments.  That is, he believed that evolution occurs when an organism uses a body part in such a way that it is altered during its lifetime and this change is then inherited by its offspring.  For example, Lamarck thought that giraffes evolved their long necks by each generation stretching further to get leaves in trees and that this change in body shape was then inherited.  Likewise, he believed that wading birds, such as herons and egrets, evolved their long legs by stretching them to remain dry.  Lamarck also believed that creatures could develop new organs or change the structure and function of old ones as a result of their use or disuse.

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| **drawing of 3 giraffes illustrating evolution based on Lamarck's incorrect idea of inheritance of acquired characteristics--the giraffes are stretching their necks to reach leaves high up in a tree.** |   | http://anthro.palomar.edu/evolve/images/Lamarck.jpg |
| Lamarck's incorrect ideaof the cause of evolution | Jean-Baptiste Lamarck1744-1829 |

Lamarck did not invent the idea of inheritance of acquired characteristics but stated it clearly and publicly in an 1809 publication entitled *Philosophie Zoologique.* It was relatively easy for the French scientist, **George Cuvier** , and other critics of Lamarck to discredit his theory.   If it was correct, the children of cowboys who have developed bowed legs as a result of a lifetime of riding horses would be born with bowed legs as well.  That, of course, does not occur.  Likewise, the children of professional weight lifters are not born with enlarged muscles.

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|   | painting of George Cuvier |
|   | George Cuvier1769-1832 |

While Lamarck's explanation of evolution was incorrect, it is unfair to label him a bad scientist.  In fact, he was at the cutting edge of biological research for his time.  He and George Cuvier were largely responsible for making biology a distinct branch of science.

Despite his criticism of Lamarck, Cuvier did not reject the idea that there had been earlier life forms.  In fact, he was the first scientist to document extinctions of ancient animals and was an internationally respected expert on dinosaurs.  However, he rejected the idea that their existence implied that evolution had occurred--he dogmatically maintained the "fixity" of species.

Cuvier advocated the theory of **catastrophism**, as did most other leading scientists of his day.  This held that there have been violent and sudden natural catastrophes such as great floods and the rapid formation of major mountain chains.  Plants and animals living in those parts of the world where such events occurred were often killed off according to Cuvier.  Then new life forms moved in from other areas.  As a result, the fossil record for a region shows abrupt changes in species.  Cuvier's explanation relied solely on scientific evidence rather than biblical interpretation.

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| **http://anthro.palomar.edu/evolve/images/lyell.jpg** |   |
| Charls Lyell    1797-1875      |   |

A careful examination of European geological deposits in the early 19th century led the English lawyer and geologist, **Charles Lyell** , to conclude that Cuvier's catastrophism theory was wrong.  He believed that there primarily have been slower, progressive changes.  In his three volume *Principles of Geology* (1830-1833), Lyell documented the fact that the earth must be very old and that it has been subject to the same sort of natural processes in the past that operate today in shaping the land.  These forces include erosion, earthquakes, glacial movements, volcanoes, and even the decomposition of plants and animals.

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|   | http://anthro.palomar.edu/evolve/images/James_Hutton.jpg |
|   | James Hutton1726-1797 |

Lyell provided conclusive evidence for the theory of **uniformitarianism**, which had been developed originally by the late 18th century Scottish geologist, **James Hutton**.  This held that the natural forces now changing the shape of the earth's surface have been operating in the past much the same way.  In other words, the present is the key to understanding the past.

This revolutionary idea was instrumental in leading Charles Darwin to his understanding of biological evolution in the 1830's.   However, it was not until the late 19th century that most educated people in the Western world finally rejected the theory of catastrophism in favor of uniformitarianism.

Today, we know that our planet has been shaped by occasional catastrophic events, such as bombardment of large meteors, in addition to the comparatively slower natural processes suggested by uniformitarianism.   All of these events have potentially affected the rate and direction of biological evolution.

*NOTE:   While George Cuvier and Charles Lyell strongly disagreed about how the earth got to be the way it is today, they both rejected the idea of biological evolution.  However, neither man accepted a traditional Biblical account of creation and a young earth.  Cuvier did not live long enough to learn about Charles Darwin's proof of evolution, but Lyell did.  He came to accept this proof in the early 1860's along with most leading scientists of that time.  Lyell also became a friend of Charles Darwin.*

***Darwin and Natural Selection***
**Most educated people in Europe and the Americas during the 19th century had their first full exposure to the concept of evolution through the writings of Charles Darwin.  Clearly, he did not invent the idea.  That happened long before he was born.  However, he carried out the necessary research to conclusively document that evolution has occurred and then made the idea acceptable for scientists and the general public.  This was not easy since the idea of evolution had been strongly associated with radical scientific and political views coming out of post-revolutionary France.  These ideas were widely considered to be a threat to the established social and political order.**

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|   | Picture of Charles Darwin portrait at age 7 |
|   | Charles Darwin at age 7 |

**Charles Darwin was born into a moderately wealthy family in Shrewsbury, England.  His father, Robert, had the largest medical practice outside of London at the time and his mother, Susannah Wedgwood, was from a family of wealthy pottery manufacturers.  She died when Charles was only 8 years old.  Thereafter, he was raised mostly by his father and doting older sisters.  Charles grew up in comparative luxury in a large house with servants.  However, this was a socially conservative time in England that set narrow limits on a young man's behavior and future possibilities.  The constraints on women in Darwin's social class were even greater.  Most were given only enough education to efficiently manage the homes of their future husbands and raise their children.  Young men were expected to go to university in order to prepare themselves to become medical doctors, military officers, or clerics in the Church of England.  Most other occupations were considered somewhat unsavory.**

**At his father's direction, Charles Darwin started university at 16 in Edinburgh, Scotland as a medical student.  He showed little academic interest in medicine and was revolted by the brutality of surgery.  Anesthesia was not used for operations until 1842.  Darwin dropped out of medical school after two years of study in 1827.  However, his knowledge of natural history was incidentally enriched in Edinburgh by the teaching of Robert Grant, a noted professor of anatomy and an avid marine biologist.  At Grant's suggestion, Darwin also became a member of *Plinian Society* for student naturalists at the University of Edinburgh.**

**Having given up on a medicine as a future career, Charles Darwin's father then sent him to Cambridge University in 1828 to pursue an *ordinary degree* program with the goal of later becoming an Anglican parson.  In Cambridge his life's direction continued its radical change.  He became very interested in the scientific ideas of the geologist Adam Sedgwick and the naturalist John Henslow with whom he spent considerable time collecting specimens from the countryside around the university.  At this time in his life, Darwin apparently rejected the concept of biological evolution, just as his mentors Sedgwick and Henslow did.  However, Darwin had been exposed to the ideas of Lamarck about evolution earlier while he was a student in Edinburgh.**

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| Picture of a portrait of Charles Darwin in his 20's |   |
| Charles Darwin1809-1882 |   |

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|   | Photo of Captain Robert Fitzroy in civilian clothes |
|   | Captain Robert Fitzroy1805-1865 |

**Following graduation from Cambridge in 1831 with a Bachelor of Arts degree, Darwin was clearly more interested in biology and geology than he was in a clerical career.  Fortunately, John Henslow was able to help him secure a berth on a British Navy mapping expedition that was going around the world on what would ultimately become a nearly five year long voyage.  Initially, Darwin's father refused to allow him to go but was eventually persuaded by Charles and even agreed to pay for his passage and for that of his man servant on the journey.  They sailed two days after Christmas in 1831 aboard the survey ship H.M.S. Beagle with Darwin acting as an unpaid naturalist and gentleman companion for the aristocratic captain, Robert Fitzroy.  Darwin was 22 years old at the time, and Fitzroy was only 4 years older.  The Beagle was a compact 90 foot long ship with a crew of 74.  There was little space, even for the captain.  Darwin shared a cramped 10 X 11 foot cabin with two other men, a cabin boy, and their belongings.  Because of the Beagle's design and small size, it was generally thought by naval men that it was ill suited for the rough seas it would encounter, especially at the southern tip of South America.  Darwin frequently suffered from sea sickness on the voyage.  Fortunately, he was able to spend most of the time on land exploring.  In fact, he was at sea for only 18 months during the nearly 5 years of the expedition.**

**Captain Fitzroy was interested in advancing science and was especially drawn to geology.  He had a surprisingly good library of over 400 books onboard the Beagle that he made available to Darwin.  It was during the beginning of the voyage that Darwin read the first volumes of Charles Lyell's "Principles of Geology" and became convinced by his proof that** [uniformitarianism](http://anthro.palomar.edu/evolve/glossary.htm#uniformitarianism) **provided the correct understanding of the earth's geological history.  This intellectual preparation, along with his research on the voyage, was critical in leading Darwin to later accept evolution.  Especially important was his 5 weeks long visit to the Galápagos Islands in the Eastern Pacific Ocean.  It was there that he made the observations that eventually led him to comprehend what causes plants and animals to evolve, but he apparently did not clearly formulate his views on this until 1837.  At the time he left the Galápagos Islands, he apparently still believed in a traditional Biblical creation of all life forms.**

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| Picture of HMS Beagle, from an 1841 watercolor |   | **map highlighting the route of H.M.S. Beagle in its around the world expedition--Britain to Brazil, Argentina, Chile, Galapagos Islands, New Zealand, Australia, South Africa, Brazil, and finally back to Britain** |   |  |
| H.M.S. Beagle(90.3 ft long, 24.5 ft. wide) | Five year voyage of H.M.S. Beagle (1831-1836) |   |

**The Galápagos Islands have species found in no other part of the world, though similar ones exist on the west coast of South America.  Darwin was struck by the fact that the birds were slightly different from one island to another.  He realized that the key to why this difference existed was connected with the fact that the various species live in different kinds of environments.**



**On returning to England, Darwin and an ornithologist associate identified 13 species of finches that he had collected on the Galápagos Islands.  This was puzzling since he knew of only one species of this bird on the mainland of South America, nearly 600 miles to the east, where they had all presumably originated.  He observed that the Galápagos species differed from each other in beak size and shape.  He also noted that the beak varieties were associated with diets based on different foods.  He concluded that when the original South American finches reached the islands, they dispersed to different environments where they had to adapt to different conditions.  Over many generations, they changed anatomically in ways that allowed them to get enough food and survive to reproduce.  This observation was verified by intensive field research in the last quarter of the 20th century.**

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| **drawings showing heads of four of the Darwin finch species highlighting the differences in their beaks** |   |  |
| Finches from the Galápagos Islands |   |

**Today we use the term adaptive radiation to refer to this sort of branching evolution in which different populations of a species become reproductively isolated from each other by adapting to different** [ecological niches](http://anthro.palomar.edu/evolve/glossary.htm#ecological_niche) **and eventually become separate species.**

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**Darwin came to understand that any population consists of individuals that are all slightly different from one another.  Those individuals having a variation that gives them an advantage in staying alive long enough to successfully reproduce are the ones that pass on their traits more frequently to the next generation.  Subsequently, their traits become more common and the population evolves.  Darwin called this "descent with modification."**

**The Galápagos finches provide an excellent example of this process.  Among the birds that ended up in arid environments, the ones with beaks better suited for eating cactus got more food.  As a result, they were in better condition to mate.  Similarly, those with beak shapes that were better suited to getting nectar from flowers or eating hard seeds in other environments were at an advantage there.  In a very real sense, nature selected the best adapted varieties to survive and to reproduce.  This process has come to be known as natural selection.**

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| painting of Thomas Malthus |   |
| Thomas Malthus   (1766-1834)    |   |

**Darwin did not believe that the environment was producing the variation within the finch populations.  He correctly thought that the variation already existed and that nature just selected for the most suitable beak shape and against less useful ones.  By the late 1860's, Darwin came to describe this process as the "survival of the fittest."   This is very different from Lamarck's incorrect idea that the environment altered the shape of individuals and that these acquired changes were then inherited.**

**Nineteenth century critics of Darwin thought that he had misinterpreted the Galápagos finch data.  They said that God had created the 13 different species as they are and that no evolution in beak shape has ever occurred.  It was difficult to conclusively refute such counter arguments at that time.  However, extensive field research since the early 1970's has proven Darwin to be correct.**

**In 1798, Thomas Malthus, an English clergyman and pioneer economist, published *Essay on the Principles of Population*.  In it he observed that human populations will double every 25 years unless they are kept in check by limits in food supply.  In 1838, Darwin read Malthus' essay and came to realize that all plant and animal populations have this same potential to rapidly increase their numbers unless they are constantly kept in check by predators, diseases, and limitations in food, water, and other resources that are essential for survival.  This fact was key to his understanding of the process of natural selection.  Darwin realized that the most fit individuals in a population are the ones that are least likely to die of starvation and, therefore, are most likely to pass on their traits to the next generation.**

**An example of evolution resulting from natural selection was discovered among "peppered" moths living near English industrial cities.  These insects have varieties that vary in wing and body coloration from light to dark.  During the 19th century, sooty smoke from coal burning furnaces killed the lichen on trees and darkened the bark.  When moths landed on these trees and other blackened surfaces, the dark colored ones were harder to spot by birds who ate them and, subsequently, they more often lived long enough to reproduce.  Over generations, the environment continued to favor darker moths.  As a result, they progressively became more common.  By 1895, 98% of the moths in the vicinity of English cities like Manchester were mostly black.  Since the 1950's, air pollution controls have significantly reduced the amount of heavy particulate air pollutants reaching the trees, buildings, and other objects in the environment.   As a result, lichen has grown back, making trees lighter in color.  In addition, once blackened buildings were cleaned making them lighter in color.  Now, natural selection favors lighter moth varieties so they have become the most common.  This trend has been well documented by field studies undertaken between 1959 and 1995 by Sir Cyril Clarke from the University of Liverpool.  The same pattern of moth wing color evolutionary change in response to increased and later decreased air pollution has been carefully documented by other researchers for the countryside around Detroit, Michigan.  While it is abundantly clear that there has been an evolution in peppered moth coloration due to the advantage of camouflage over the last two centuries, it is important to keep in mind that this story of natural selection in action is incomplete.  There may have been additional natural selection factors involved.**

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| drawing of dark and light colored peppered moths on a tree with dark colored bark and a tree with light bark  Dark moths on light colored bark are  easy targets for  hungry birds but are  hidden on pollution darkened trees. |   |  |

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**Darwin's use of the phrase "survival of the fittest" is frequently misunderstood.  Many people assume that "the fittest" refers to the strongest, biggest, or smartest and most cunning individuals.  This may or may not be the case.  From an evolutionary perspective, the fittest individuals are simply the ones who have the combination of traits that allow them to survive and produce more offspring that in turn survive to reproduce.  In fact, they may be relatively weak, small, and not particularly intelligent.  What makes an individual fit all depends on the environment at the time and the combination of traits that are most suited to flourishing in it.  In the case of Darwin's finches, specialized beaks provided the advantage.  However, in a changing environment, it is often the versatile generalist who has the greatest success.**

**Darwin did not believe that evolution follows a predetermined direction or that it has an inevitable goal.  His explanation that evolution occurs as a result of natural selection implied that chance plays a major role.  He understood that it is a matter of luck whether any individuals in a population have variations that will allow them to survive and reproduce.  If no such variations exist, the population rapidly goes extinct because it cannot adapt to a changing environment.  Unlike Lamarck, Darwin did not believe that evolution inevitably produces more complex life forms and that the ultimate result of this process is humans.  These were shocking, revolutionary ideas even for scientists who accepted evolution.**

**Darwin did not rush his ideas about evolution and natural selection into print.  He first concentrated his efforts on writing the account of his around the world voyage on the Beagle and analyzing the many preserved animal and plant specimens and extensive notes that he brought back with him.  This occupied him for more than 10 years.  An additional factor that may have held him back from publishing his ideas about evolution was the widespread Christian evangelical fervor in England during the 1830's and 1840's.  He could have been charged with sedition and blasphemy for widely publishing his unpopular theory.**

**After returning from the voyage of the Beagle, Darwin settled down in England, married Emma Wedgwood (his wealthy first cousin), raised a large family, and quietly continued his research at his newly purchased country home 16 miles south of London.  In 1842 he wrote a 35 page summary of his theory about evolution.  This was expanded to a 230 page manuscript in 1844, but it was not published and apparently was only known to a few people in British scientific circles.  Darwin busied himself over the next two decades establishing his reputation as an important naturalist by growing and studying orchids, pigeons, earthworms, and other organisms at his home.  He spent 8 of these years studying and writing about barnacles that people had sent him from around the world.**

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| Picture of a portrait of Emma Darwin as a young woman |   | Photograph of Down House from the back garden |   | photo of Charles Darwin in late middle age |
| Emma Darwin1808-1896  |   |     Down House--Charles and Emma Darwin's country    home where he wrote his major publications and        their family lived contentedly for 40 years. | Charles Darwin1809-1882  |

**It was not until he was 50 years old, in 1859, that Darwin finally published his theory of evolution in full for his fellow scientists and for the public at large.  He did so in a 490 page book entitled *On the Origin of Species*.  It was very popular and controversial from the outset.  The first edition came out on November 24, 1859 and sold out on that day.  It went through six editions by 1872.  The ideas presented in this book were expanded with examples in fifteen additional scientific books that Darwin published over the next two decades.**

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| http://anthro.palomar.edu/evolve/images/Wallace.jpg |   |
| Alfred Wallace1823-1913 |   |

**What finally convinced Darwin that he should publish his theory in a book for the general educated public was the draft of an essay that he received in the summer of 1858 from a younger British naturalist named Alfred Wallace** **, who was then hard at work collecting biological specimens in Southeast Asia for sale to museums and private collectors.  Darwin was surprised to read that Wallace had come upon essentially the same explanation for evolution.  Being a fair man, Darwin insisted that Wallace also get credit for the natural selection theory during debates over its validity that occurred at a meeting of the British Association for the Advancement of Science at Oxford University in 1860.  We now know that Darwin deserves most of the credit.  In 1837, one year after he returned from the voyage on the Beagle, he made detailed notes on the idea of evolution by means of natural selection.  At that time, Wallace was only 14 years old.  In addition, it was Darwin's book, rather than Wallace's essay, that had the most impact on the Victorian public.  Darwin not only described the process of natural selection in more detail, but he also gave numerous examples of it.  It was his *On the Origin of Species* that convinced most scientists and other educated people in the late 19th century that life forms do change through time.  This prepared the public for the acceptance of earlier human species and of a world much older than 6000 years.**

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|   | http://anthro.palomar.edu/evolve/images/Mendel.jpg |
|   | Gregor Mendel1822-1884 |

**Both Darwin and Wallace failed to understand an important aspect of natural selection.  They realized that plant and animal populations are composed of individuals that vary from each other in physical form.  They also understood that nature selects from the existing varieties those traits that are most suited to their environment.  If natural selection were the only process occurring, each generation should have less variation until all members of a population are essentially identical, or clones of each other.  That does not happen.  Each new generation has new variations.  Darwin was aware of this fact, but he did not understand what caused the variation.  The first person to begin to grasp why this happens was an obscure Central European monk named Gregor Mendel** **.  Through plant breeding experiments carried out between 1856 and 1863, he discovered that there is a recombination of parental traits in offspring.  Sadly, Darwin and most other 19th century biologists never knew of Mendel and his research.  It was not until the beginning of the 20th century that Mendel's pioneer research into genetic inheritance was rediscovered.  This was long after his death.   He never received the public acclaim that was eventually showered on Darwin during his lifetime.**

**Charles Darwin's convincing evidence that evolution occurs was very threatening to many Christians who believed that people were created specially by God and that they have not changed biologically since that creation.  The idea that there could have been prehistoric humans who were anatomically different from us was rejected for similar reasons.  However, Charles Lyell's geological evidence that the earth must be much older than 6,000 years along with the rapidly accumulating fossil record of past evolution convinced educated lay people in the 1860's to think what had been unthinkable earlier.**

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| painting of Boucher de Perthes in 1832 |
| Boucher de Perthes   1788-1868    |

**Archaeological confirmation of the existence of prehistoric Europeans had been accumulating since the 1830's.  However, until the late 1850's, it had been widely rejected or misinterpreted.  Much of this evidence had been collected by Jacques Boucher** Crèvecoeur **de Perthes , a customs officer in northern France during the early 1800's.  His hobby was collecting ancient stone tools from deep down in the Somme River gravel deposits.  Since he found these artifacts in association with the bones of extinct animals, he concluded that they must have been made at the time that those animals lived.**

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|   | 19th century drawing of a well shaped prehistoric hand ax in front and side views |
|   | Prehistoric artifact incorrectly thoughtto be a "lightning bolt remnant"   |

**Boucher de Perthes tried to publish his findings in 1838.  They were rejected by all important scientists and scientific journals.  The prehistoric stone tools usually were dismissed as being only "lightning stones" (i.e., the remnants of lightning bolts).  However, by 1858, his claims were beginning to be accepted by some enlightened Western European scientists.  Darwin's publication of *On the Origin of Species* the following year convinced even more educated people that Boucher de Perthes had been right.**

**Darwin's popularizing the idea of evolution also made it possible for scientists to begin to accept that some of the makers of Boucher de Perthes' prehistoric tools had already been discovered and that their bones were in museums.  These bones had been found in several Western European countries during the first half of the 19th century.  However, they had all been dismissed as being from odd looking modern people.  During the 1860's, some were correctly determined to be from an earlier species or variety of people who had lived during the last ice age--i.e., long before recorded history.  We now know that these ancient people were mostly Neandertals, who lived about 150,000-28,000 years ago.**

***NOTE:   Charles Darwin was an active collector of plant and animal specimens and a prodigious note taker on the voyage of H.M.S. Beagle.  By the time the ship returned to England in 1836, he had accumulated 5,436 plant and animal specimens that had been dried or preserved in alcohol.  He had 368 pages of notes on plants and animals as well as 1,383 pages of geological observations.  In addition, he had a 770 page diary that was the basis for his later popular book of his narrative on the voyage ("***[*Journal of Researches Into the Natural History and Geology of the Countries Visited During the Voyage of H.M.S. Beagle Round the World, Under the Command of Capt. Fitz Roy, R.N.*](http://darwin-online.org.uk/content/frameset?itemID=F14&viewtype=text&pageseq=1)***").***

***NOTE:   From the time that Charles Darwin published "On the Origin of Species" in 1859 on up to the present, the presumptions of many people led them to misread the title.  They assumed that it was "On the Origin of the Species".  The implication of inadvertently adding "the" is that his book was about human evolution.  In fact, that was not the case, though it had implications for human evolution.  It focused on non-human animals and the mechanisms of evolution.  He did not pointedly address the question of human evolution until the publication of his 1871 book "Descent of Man and Selection in Relation to Sex".***

***NOTE:   The phrase "survival of the fittest" was apparently first used in 1851 by the influential British philosopher Herbert Spencer (1820-1903) as a central tenet of what later became known as "Social Darwinism."  He misapplied Darwin's idea of natural selection to justify European domination and colonization of much of the rest of the world.  Social Darwinism was also widely used to defend the unequal distribution of wealth and power in Europe and North America at the time.  Poor and politically powerless people were thought to have been failures in the natural competition for survival.  Subsequently, helping them was seen as a waste of time and counter to nature.  From this perspective, rich and powerful people did not need to feel ashamed of their advantages because their success was proof that they were the most fit in this competition.  Despite misgivings by Alfred Wallace and other naturalists, Charles Darwin began to use "survival of the fittest" as a synonym for "natural selection" in the 5th edition of Origin of Species, which was published in 1869.***

***NOTE:   H.M.S. Beagle, the famous ship that took Charles Darwin on his 1831-1836 voyage around the world, had a rather mundane history following her return to England.****She was transferred by the British Navy to the Customs and Excise Department and was used to catch smugglers along the southeast coast of England.  The Beagle was finally sold for scrap in 1870 after 50 years of service.*

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| Extinctions: Georges Cuvier By the 1700s, fossils had been inducted into the living world. Instead of being produced by rocks themselves, fossils were recognized as the remains of animals or plants. They looked too much like particular living species to be anything else. As the eighteenth century wore on, some fossils emerged that could not be tied so neatly to the known living species. Elephants, for example, had left fossils in Italy, where they could no longer be found. Yet elephants still lived in Africa, and naturalists assumed that other fossils had living counterparts of their own in some remote part of the world. But, at the end of the century, a French naturalist offered an astonishing revelation: some species had actually vanished from the face of the Earth.

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| Georges Cuvier | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | Georges Cuvier (1769-1832) joined the fledgling National Museum in Paris in 1795, and quickly became the world's leading expert on the anatomy of animals. He then used that knowledge to interpret fossils with unprecedented insight. Legend has it that sometimes even a few fragments of bones were enough for him to reconstruct the complete anatomy of a previously unknown species with uncanny accuracy. Armed with this expertise, Cuvier waded into the debate over whether species could become extinct. |

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| first mosasaur fossils |
| This print shows the recovery of the first mosasaur fossils in 1780. Cuvier used the fossils to support his radical ideas on extinction. |

A few earlier naturalists, such as [Buffon](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_06), had argued that species might become extinct. But for many people in Cuvier's day, the idea of extinction was religiously troubling. If God had created all of nature according to a divine plan at the beginning of the world, it would seem irrational for Him to let some parts of that creation die off. If life consisted of a Great Chain of Being, extending from ocean slime to humans to angels, extinctions would remove some of its links.

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| http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | Mammoth jaw comparison |
| A 1798 paper by Cuvier contained this drawing showing the differences between the lower jaws of a mammoth (top) and an Indian elephant. These differences supported the idea that mammoths were indeed extinct. |

Cuvier carefully studied elephant fossils found near Paris. He discovered that their bones were indisputably distinct from those of living elephants in Africa and India. They were distinct even from fossil elephants in Siberia. Cuvier scoffed at the idea that living members of these fossil species were lurking somewhere on Earth, unrecognized—they were simply too big. Instead, Cuvier declared that they were separate species that had vanished. He later studied many other big mammal fossils and demonstrated that they too did not belong to any species alive today. The fossil evidence led him to propose that periodically the Earth went through sudden changes, each of which could wipe out a number of species. Cuvier established extinctions as a fact that any future scientific theory of life had to explain. In [Darwin's](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_14) theory, species that did not adapt to changing environments or withstand the competition of other species faced annihilation. Darwin did not, however, accept all of Cuvier's ideas on extinctions. Like [Charles Lyell](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_12) before him, he doubted that species went extinct in great "catastrophes." Just as the planet's geology changed gradually, so did its species become extinct gradually as new species were formed. Background extinction *and* catastropheOn this score, Cuvier has been somewhat vindicated. Perhaps 99% of all species that ever existed on Earth are now extinct. Most of those extinct species disappeared in a Darwinian trickle—what paleontologists call "background extinctions." But several times over the past 600 million years, life has experienced "mass extinctions", in which half or more of all species alive at the time disappeared in fewer than two million years—a blink of a geological eye. The causes may include asteroids, volcanoes, or relatively fast changes in sea level. These extinctions mark some of the great transitions in life, when new groups of species got the opportunity to take over the niches of old ones. Mammals, for example, only dominated the land after giant dinosaurs vanished 65 million years ago in the Cretaceous-Tertiary extinction. We humans, in other words, are the children of extinctions.

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| Mass and background extinctionLife’s history has been marked by both catastrophic extinction events (red spikes) and constant background extinction (yellow).Uniformitarianism: Charles Lyell

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| gradual change by erosion |
| Discrete rock layers containing different fossils reinforced the idea that the Earth's history could be divided into ages marked by catastrophic change. However, gradual change, like that caused by erosion, has also played an important role in the Earth's history. |

Thanks to the pioneering work of researchers such as [William Smith](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_11), geologists in the early 1800s were able to swiftly organize rock formations into a single colossal record of Earth's history. Many geologists saw in this record a stormy epic, one in which our planet had been convulsed repeatedly by abrupt changes. Mountains were built in catastrophic instants, and in the process whole groups of animals became extinct and were replaced by new species. Giant tropical plants, for example, left their fossils in northern Europe during the Carboniferous Period, never to be seen there again. Earth's history might not fit a strict Biblical narrative any longer, but these revolutions seemed to be a sign that it did have a direction. From its formation, catastrophes altered the planet’s surface step by step leading towards the present Earth. Life, likewise, had its own arrow through time.CatastrophismEven before this geological evidence had emerged, some naturalists had already claimed that Earth's history had a direction. [Buffon](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_06), and later the physicist [Joseph Fourier](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=Fourier%2C+Joseph), both claimed that the Earth had begun as a hot ball of molten rock and had been cooling through time. Fourier argued that the tropical plants of Europe must have lived during those warmer times. Some geologists suggested that the cooling of the planet occasionally triggered violent, sudden uplifts of mountains and volcanic eruptions.

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| Charles Lyell |  |

"Catastrophism," as this school of thought came to be known, was attacked in 1830 by a British lawyer-turned-geologist named Charles Lyell (1797-1875). Lyell started his career studying under the catastrophist [William Buckland](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=Buckland%2C+William) at Oxford. But Lyell became disenchanted with Buckland when Buckland tried to link catastrophism to the Bible, looking for evidence that the most recent catastrophe had actually been Noah's flood. Lyell wanted to find a way to make geology a true science of its own, built on observation and not susceptible to wild speculations or dependent on the supernatural. |

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| http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | The rock cycle |
| The ideas of Hutton and Lyell led to an understanding of "the rock cycle" as we know it today. |

Gradual changeFor inspiration, Lyell turned to the fifty-year-old ideas of a Scottish farmer named [James Hutton](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=Hutton%2C+James). In the 1790s, Hutton had argued that the Earth was transformed not by unimaginable catastrophes but by imperceptibly slow changes, many of which we can see around us today. Rain erodes mountains, while molten rock pushes up to create new ones. The eroded sediments form into layers of rock, which can later be lifted above sea level, tilted by the force of the uprising rock, and eroded away again. These changes are tiny, but with enough time they could produce vast changes. Hutton therefore argued that the Earth was vastly old — a sort of perpetual-motion machine passing through regular cycles of destruction and rebuilding that made the planet suitable for mankind.

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| Valley formed by erosion | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif |
| Lyell found evidence that valleys were formed through the slow process of erosion, not by catastrophic floods. |

Lyell traveled through Europe to find more evidence that gradual changes, the same we can see happening today, had produced the features of the Earth's surface. He found evidence for many rises and falls of sea level, and of giant volcanoes built on top of far older rocks. Processes such as earthquakes and eruptions, which had been witnessed by humans, were enough to produce mountain ranges. Valleys were not the work of giant floods but the slow grinding force of wind and water.Uniform Processes of ChangeLyell's version of geology came to be known as uniformitarianism, because of his fierce insistence that the processes that alter the Earth are uniform through time. Like Hutton, Lyell viewed the history of Earth as being vast and directionless. And the history of life was no different.

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| http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | Tenerife, Canary Islands |

Lyell crafted a powerful lens for viewing the history of the Earth. On Darwin's voyage aboard the *Beagle*, for example, he was able to decipher the history of the Canary Islands (right) by applying Lyell's ideas to the volcanic rock he encountered there. Today satellite measurements reveal that mountains may rise an inch a year, while radioactive clocks help show how they've been rising that way for millions of years. But Lyell could never have grasped the mechanism — plate tectonics — that makes this kind of geological change happen.Yet geologists today also know that some of the factors that changed the Earth in the past cannot be seen at work today. For example, the early Earth was pummeled by gigantic hunks of solar debris, some as big as Mars. For the first one or two billion years of Earth's history, plate tectonics didn't even exist as we know it today.Lyell had an equally profound effect on our understanding of life's history. He influenced Darwin so deeply that Darwin envisioned evolution as a sort of biological uniformitarianism. Evolution took place from one generation to the next before our very eyes, he argued, but it worked too slowly for us to perceive. |

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| Early Concepts of Evolution: Jean Baptiste Lamarck

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| Jean Baptiste Lamarck | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif |

[Darwin](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_14) was not the first naturalist to propose that species changed over time into new species—that life, as we would say now, evolves. In the eighteenth century, [Buffon](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_06) and other naturalists began to introduce the idea that life might not have been fixed since creation. By the end of the 1700s, paleontologists had swelled the fossil collections of Europe, offering a picture of the past at odds with an unchanging natural world. And in 1801, a French naturalist named Jean Baptiste Pierre Antoine de Monet, Chevalier de Lamarck took a great conceptual step and proposed a full-blown theory of evolution.Lamarck started his scientific career as a botanist, but in 1793 he became one of the founding professors of the Musee National d'Histoire Naturelle as an expert on invertebrates. His work on classifying worms, spiders, molluscs, and other boneless creatures was far ahead of his time.

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| Change through use and disuseLamarck was struck by the similarities of many of the animals he studied, and was impressed too by the burgeoning fossil record. It led him to argue that life was not fixed. When environments changed, organisms had to change their behavior to survive. If they began to use an organ more than they had in the past, it would increase in its lifetime. If a giraffe stretched its neck for leaves, for example, a "nervous fluid" would flow into its neck and make it longer. Its offspring would inherit the longer neck, and continued stretching would make it longer still over several generations. Meanwhile organs that organisms stopped using would shrink.  | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | Giraffe neck extensionLamarck believed that the long necks of giraffes evolved as generations of giraffes reached for ever higher leaves. |

Organisms driven to greater complexityThis sort of evolution, for which Lamarck is most famous today, was only one of two mechanisms he proposed. As organisms adapted to their surroundings, nature also drove them inexorably upward from simple forms to increasingly complex ones. Like Buffon, Lamarck believed that life had begun through spontaneous generation. But he claimed that new primitive life forms sprang up throughout the history of life; today's microbes were simply "the new kids on the block."

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| Lamarck's arrow of complexity |
| Lamarck also proposed that organisms were driven from simple to increasingly more complex forms. |

Evolution by natural processesLamarck was mocked and attacked by [Cuvier](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_08) and many other naturalists of his day. While they questioned him on scientific grounds, many of them were also disturbed by the theological implications of his work. Lamarck was proposing that life took on its current form through natural processes, not through miraculous interventions. For British naturalists in particular, steeped as they were in natural theology, this was appalling. They believed that nature was a reflection of God's benevolent design. To them, it seemed Lamarck was claiming that it was the result of blind primal forces. Shunned by the scientific community, Lamarck died in 1829 in poverty and obscurity. But the notion of evolution did not die with him. The French naturalist Geoffroy St. Hilaire would champion another version of evolutionary change in the 1820s, and the British writer Robert Chambers would author a best-selling argument for evolution in 1844: Vestiges of a Natural Creation. And in 1859, Charles Darwin would publish the Origin of Species.

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| Lamarck vs. Darwin  | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif |

Different from DarwinIn many ways, Darwin's central argument is very different from Lamarck's. Darwin did not accept an arrow of complexity driving through the history of life. He argued that complexity evolved simply as a result of life adapting to its local conditions from one generation to the next. He also argued that species could go extinct rather than change into new forms. But Darwin also relied on much the same evidence for evolution that Lamarck did (such as [vestigial structures](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=vestigial+structure) and [artificial selection](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=artificial+selection) through breeding). And Darwin wrongly accepted that changes acquired during an organism's lifetime could be passed on to its offspring. Lamarckian inheritance remained popular throughout the 1800s, in large part because scientists did not yet understand how heredity works. With the discovery of genes, it was finally abandoned for the most part. But Lamarck, whom Darwin described as "this justly celebrated naturalist," remains a major figure in the history of biology for envisioning evolutionary change for the first time. |

Developmental Similarities: Karl von Baer

How does life begin? At the dawn of the nineteenth century, naturalists were staring through microscopes in hopes of finding the answer. In the process, they discovered some peculiar things about embryos. A chicken may look very different from a fish, but their embryos share some striking similarities. They both develop from a single cell into tube-shaped bodies, for example. They share many traits early on, such as a set of arching blood vessels in their necks. In fish, the vessels retain this arrangement, so that they can take in oxygen from their gills. But in chickens—as well as mammals like us, amphibians, and reptiles—they are reworked into a very different anatomy suited to getting oxygen through lungs.

In Germany, where much of this study was done, some researchers claimed that these similarities were signs that life formed a series from simple forms to lofty ones (the loftiest being, of course, ourselves). As embryos we pass through this series—we "recapitulate" it—on our way to becoming human. We started out life as a worm, became a fish (complete with gill arches), a reptile, and so on. Some naturalists even claimed that recapitulation was evidence that life had changed through time, as higher and higher forms emerged on Earth.

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| Karl von Baer | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | von Baer: Recapitulation is kaputIn 1828, the Estonian-born embryologist Karl von Baer launched a withering attack on recapitulation. A careful look at embryos revealed that it was impossible to arrange them in any meaningful series. From the earliest stages, vertebrates all share an anatomy that invertebrates such as insects or worms never acquire. And even within vertebrates, there are facts that clash with recapitulation. A human does not develop a wing or a hoof before forming a hand—humans, birds, and horses all begin with limb buds, which then diverge into different adult limbs. |

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| Compelling evidence for evolutionBaer was no fan of evolution, and so it was much to his chagrin that [Darwin](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_14) used his work to provide some of the most compelling evidence in *Origin of Species*. A species inherits its developmental program from its ancestors, and so two closely related species would be expected to have similar—but not necessarily identical—embryos. Over time, as lineages evolve further away from each other, [natural selection](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=natural+selection) modifies their embryos in various ways, but some vestiges of their common ancestry survive. That's why we still bear a limited resemblance to fish in our early embryonic stages. Darwin did not argue that life was arrayed in a linear series from lower to higher; instead, he saw life branching like a tree as new species emerged.That branching was reflected in the similar paths of development that ultimately produced hooves, claws, and hands. | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | ladder vs. tree analogySome researchers believed life developed in a linear fashion, from simple to more complex forms (left). Darwin compared the emergence of new species to the branching of a tree (right). |

What about Baer's claim that vertebrates couldn't be aligned with invertebrate animals? Embryologists working in the mid-1800s showed that the division was not unbridgeable. Some invertebrates known as sea squirts, for example, develop the same kind of stiff rod that vertebrates form in their back as embryos, known as a notochord. In vertebrates the notochord turns into the disks between the vertebrae. If this were in fact a sign of common ancestry, you'd expect sea squirts to be close relatives of vertebrates. And indeed, studies on the [DNA](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=DNA) of sea squirts show that they are in fact the closest invertebrate relatives of vertebrates yet known.

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| Tunicate larva diagram | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | Tunicate larva photo |
| Since Baer's time, tunicates (several varieties of adults, left) have been found to be a bridge between invertebrates and vertebrates. Tunicate larvae (right) have a notochord much like that found in vertebrate embryos. |
| Biostratigraphy: William Smith

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| William Smith | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif |

At the end of the eighteenth century, geologists still had a confused perception of the rocks they studied. [Steno](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_04) had shown in the 1600s that rocks could form in horizontal layers over time, which might later be carved away to expose old rock once again. But geologists had great difficulty reconstructing the original order of the layers by looking at the surviving rock. That began to change around 1800, thanks in large part to an obscure British canal surveyor named William Smith (above left).

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Relative dating of rocks using fossilsSmith, who had little formal education, traveled throughout England as a surveyor and spent six years supervising the digging of the Somerset Canal in southwestern England. Along the way he became well acquainted with the rocks through which he cut the canals. He was surprised to find that the fossils in the layers often were arranged in the same distinctive order from the bottom to the top of the rocks. And as he traveled across England, he discovered the same sequences of fossils in rock layers. Each type of animal, he realized, had a widespread existence for a particular span of time, a span that partially overlapped with that of other animals. That made it possible for Smith to recognize the order in which rocks had been formed throughout much of England.

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| Smith's mapSmith's geological map of England. Different colors represent rocks of different geologic periods of time.   |  |

Smith began to make the first geological map of England. It took sixteen years to publish it, but the geologists of his day, drawn from the upper classes, spurned this unpolished pioneer. For years after publishing his map, Smith lived in anonymous poverty. Only in 1831 did a new generation of geologists appreciate Smith's contribution. In that year the Geological Society of London awarded him the Wollaston Medal, their highest prize.Triggering a revolutionBy the time Smith received the Wollaston Medal, his map had helped trigger a revolution in geology. Geologists used his methods to discover even older geological formations whose outcrops were scattered across England. Meanwhile on the continent, [Georges Cuvier](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_08) and [Alexandre Brongniart](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=Brongniart%2C+Alexandre) used much the same method to decipher the rocks around Paris. It became inescapably clear to geologists that Earth and its life were far older than a few thousand years.Chapters in the history of lifeTheir maps also allowed them to organize the history of life into a series of chapters, from the Cambrian with its bizarre invertebrates to the dinosaurs of the Jurassic to the mammals of more recent times. Life in each stage was a unique collection of species. Exactly how it had changed from one stage to the next was a matter of fierce debate. [Adam Sedgwick](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=Sedgewick%2C+Adam), a geologist at Cambridge University, suggested that God somehow brought new forms of life into existence at the beginning of each geological age. [Richard Owen](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=Owen%2C+Richard), England's leading anatomist at the time, argued that over time God created new species by modifying a basic anatomical idea, an "archetype." Darwin, finally, recognized that fossils recorded the evolution and [extinction](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=extinction) of life, as [natural selection](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=natural+selection) and other natural factors changed species through time. |

Discrete Genes Are Inherited: Gregor Mendel

Throughout the nineteenth century, heredity remained a puzzle to scientists. How was it that children ended up looking similar to, but not exactly like, their parents? These questions fascinated and frustrated [Charles Darwin](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_14) deeply. After all, heredity lies at the heart of evolution. The variations in each generation are the raw material for [natural selection](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=natural+selection), while the continuity from one generation to the next allows the changes wrought by natural selection to have long-term effects. Darwin himself proposed that each cell in an animal's body released tiny particles that streamed to the sexual organs, where they combined into eggs or sperm. They would then blend together when the animal mated. But "pangenesis," as Darwin called it, didn't hold up to scrutiny.

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| http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | Gregor Mendel  |

Ironically, it was just as Darwin was publishing the *Origin of Species* that someone got the first real glimpse of the biological machinery behind heredity. In a secluded monastery in what is now the Czech Republic, a monk named Gregor Mendel was studying heredity in a garden of peas. Mendel, the son of a farmer, had always been interested in plants, and while at the University of Vienna he had been trained in mathematics and learned how to design experiments and analyze data. In the 1850s, he decided to run an experiment to better understand what kept species distinct and what made it possible for hybrids to form. He bred thousands of pea plants and recorded how traits were passed on from one generation to the next.

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| Smooth and wrinkled peas  | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif |

Trait inheritance
Mendel selected 22 different varieties of peas and interbred them, keeping track of seven different traits, such as pea texture — smooth or wrinkled. Mendel found that when he hybridized smooth and wrinkled peas, he produced peas that were all smooth. But if he then produced a new generation of peas from the hybrids, a quarter of the peas were wrinkled.

Mendel proposed that the peas were not blending their "wrinkled" and "smooth" traits together. Each hybrid pea inherited both traits, but only the smooth trait became visible. In the next generation, the traits were handed down again, and a quarter of the new peas inherited two "wrinkled" traits, which made them wrinkled. Mendel had discovered what later scientists called "dominant" and "recessive" [alleles](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=allele).

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| http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | Hawkweed |
| Mendel's experiments with hawkweed did not yield results consistent with his work on peas. |

Mendel's work goes unrecognized
Mendel tried to drum up interest in his results but to no avail. Part of the problem was that botanists of Mendel's time were not accustomed to statistics being applied to natural history, and so they couldn't recognize the importance of Mendel's discovery. And when Mendel tried to replicate his results with hawkweed, he failed — not because his original insights were wrong, but because the genetics of hawkweed are very peculiar. Nevertheless, the patterns that Mendel saw did apply to many organisms and were there in nature for anyone to see. Darwin himself noted a three-to-one ratio in the colors of snapdragons. But for all his genius, Darwin didn't realize the importance of that ratio.

Mendel abandoned his experiments in the 1860s and turned his attentions to running his monastery. When he died in 1884, he was remembered as a puttering monk with a skill for breeding plants. It was only some 15 years after his death that scientists realized that Mendel had revealed the answer to one of life's greatest mysteries.

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| Natural Selection: Charles Darwin & Alfred Russel Wallace

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| Charles Darwin |  |

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|  | Darwin's finches |
| A visit to the Galapagos Islands in 1835 helped Darwin formulate his ideas on natural selection. He found several species of finch adapted to different environmental niches. The finches also differed in beak shape, food source, and how food was captured. |

The genius of Darwin (left), the way in which he suddenly turned all of biology upside down in 1859 with the publication of the *Origin of Species*, can sometimes give the misleading impression that the theory of evolution sprang from his forehead fully formed without any precedent in scientific history. But as earlier chapters in this history have shown, the raw material for Darwin's theory had been known for decades. Geologists and paleontologists had made a compelling case that life had been on Earth for a long time, that it had changed over that time, and that many species had become extinct. At the same time, embryologists and other naturalists studying living animals in the early 1800s had discovered, sometimes unwittingly, much of the best evidence for Darwin's theory. Pre-Darwinian ideas about evolutionIt was Darwin's genius both to show how all this evidence favored the evolution of species from a common ancestor and to offer a plausible mechanism by which life might evolve. Lamarck and others had promoted evolutionary theories, but in order to explain just how life changed, they depended on speculation. Typically, they claimed that evolution was guided by some long-term trend. Lamarck, for example, thought that life strove over time to rise from simple single-celled forms to complex ones. Many German biologists conceived of life evolving according to predetermined rules, in the same way an embryo develops in the womb. But in the mid-1800s, Darwin and the British biologist Alfred Russel Wallace independently conceived of a natural, even observable, way for life to change: a process Darwin called [natural selection.](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=natural+selection)The pressure of population growthInterestingly, Darwin and Wallace found their inspiration in economics. An English parson named [Thomas Malthus](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_07) published a book in 1797 called *Essay on the Principle of Population* in which he warned his fellow Englishmen that most policies designed to help the poor were doomed because of the relentless pressure of population growth. A nation could easily double its population in a few decades, leading to famine and misery for all.When Darwin and Wallace read Malthus, it occurred to both of them that animals and plants should also be experiencing the same population pressure. It should take very little time for the world to be knee-deep in beetles or earthworms. But the world is not overrun with them, or any other species, because they cannot reproduce to their full potential. Many die before they become adults. They are vulnerable to droughts and cold winters and other environmental assaults. And their food supply, like that of a nation, is not infinite. Individuals must compete, albeit unconsciously, for what little food there is. |

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| http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | Pigeon breeding |
| The carrier pigeon (bottom left) and the Brunner pouter (bottom right) were derived from the wild rock pigeon (top). |

Selection of traitsIn this struggle for existence, survival and reproduction do not come down to pure chance. Darwin and Wallace both realized that if an animal has some trait that helps it to withstand the elements or to breed more successfully, it may leave more offspring behind than others. On average, the trait will become more common in the following generation, and the generation after that. As Darwin wrestled with [natural selection](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=natural+selection) he spent a great deal of time with pigeon breeders, learning their methods. He found their work to be an analogy for evolution. A pigeon breeder selected individual birds to reproduce in order to produce a neck ruffle. Similarly, nature unconsciously "selects" individuals better suited to surviving their local conditions. Given enough time, Darwin and Wallace argued, natural selection might produce new types of body parts, from wings to eyes. |

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| http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | Alfred Russel Wallace |

Darwin and Wallace develop similar theoryDarwin began formulating his theory of natural selection in the late 1830s but he went on working quietly on it for twenty years. He wanted to amass a wealth of evidence before publicly presenting his idea. During those years he corresponded briefly with Wallace (right), who was exploring the wildlife of South America and Asia. Wallace supplied Darwin with birds for his studies and decided to seek Darwin's help in publishing his own ideas on evolution. He sent Darwin his theory in 1858, which, to Darwin's shock, nearly replicated Darwin's own.

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| The Origin of Species | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif |

[Charles Lyell](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_12) and Joseph Dalton Hooker arranged for both Darwin's and Wallace's theories to be presented to a meeting of the Linnaean Society in 1858. Darwin had been working on a major book on evolution and used that to develop *On the Origins of Species*, which was published in 1859. Wallace, on the other hand, continued his travels and focused his study on the importance of biogeography.The book was not only a best seller but also one of the most influential scientific books of all time. Yet it took time for its full argument to take hold. Within a few decades, most scientists accepted that evolution and the descent of species from common ancestors were real. But natural selection had a harder time finding acceptance. In the late 1800s many scientists who called themselves Darwinists actually preferred a Lamarckian explanation for the way life changed over time. It would take the discovery of [genes](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=gene) and [mutations](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=mutation) in the twentieth century to make natural selection not just attractive as an explanation, but unavoidable. |

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| Early Evolution and Development: Ernst Haeckel

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|  | Mouse embryo and tunicate notochordsBoth vertebrate embryos and tunicate larvae have notochords (colored blue in the mouse; a thin dark line in the tunicate).  |

Darwin showed how the mysterious similarities between embryos made ample sense if life evolved by natural selection. With the publication of the *Origin of Species*, many scientists then asked the next logical question: did embryonic development record the actual evolutionary history of their species? Initially, the prospects were promising. Some invertebrates known as tunicates or sea squirts, for example, develop the same kind of stiff rod, known as a notochord, that vertebrates form in their back as embryos. In vertebrates the notochord turns into the disks between the vertebrae. Researchers speculated that a sea-squirt-like animal might have been the ancestor of vertebrates. (Recent DNA studies show that sea squirts are in fact the closest known invertebrate relatives of vertebrates.) |

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| Ernst Haeckel |  |

Ontogeny recapitulates phylogeny...or does it?The evolutionary study of embryos reached a peak in the late 1800s thanks primarily to the efforts of one extraordinarily gifted, though not entirely honest, scientist named Ernst Haeckel (left). Haeckel was a champion of Darwin, but he also embraced the pre-Darwinian notion that life formed a series of successively higher forms, with embryos of higher forms "recapitulating" the lower ones. Haeckel believed that, over the course of time, evolution added new stages to produce new life forms. Thus, embryonic development was actually a record of evolutionary history. The single cell corresponded to amoeba-like ancestors, developing eventually into a sea squirt, a fish, and so on. Haeckel, who was adept at packaging and promoting his ideas, coined both a name for the process — "the Biogenetic Law" — as well as a catchy motto: "Ontogeny recapitulates phylogeny."Haeckel was so convinced of his Biogenetic Law that he was willing to bend evidence to support it. The truth is that the development of embryos does not fit into the strict progression that Haeckel claimed. Echidnas, for example, develop their limbs much later than most other mammals. But in his illustrations of echidna embryos, Haeckel deceptively omitted limb buds at early stages, despite the fact that limb buds do exist then. In Haeckel's own day, some biologists recognized his sleights of hand, but nevertheless the Biogenetic Law became very popular, and Haeckel's illustrations even found their way into biology textbooks.The biogenetic law is brokenBy the turn of the century, scientists had discovered many cases that defied Haeckel's so-called law. His followers tried to cast them as exceptions that proved the rule. But Haeckel's final downfall came with the rise of genetics and the modern synthesis. Haeckel, after all, was promoting a basically Lamarckian notion that evolution had a built-in direction towards "higher" forms. But genes, it was soon discovered, controlled the rate and direction of embryonic development. Individual genes can mutate and cause different changes to the way embryos grow — either adding new stages at any point along their path, or taking them away, speeding up development or slowing it down.

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| Haeckel's tree and modern phylogeny |
| Haeckel imagined humans ("Menschen" in German) to be the "highest" form of life, placing them at the top of his tree of life (left); at right, how the same anthropoid relationships might be shown today. Note that modern evidence suggests that the phylogeny proposed by Haeckel and represented here is incorrect. |

Embryos do reflect the course of evolution, but that course is far more intricate and quirky than Haeckel claimed. Different parts of the same embryo can even evolve in different directions. As a result, the Biogenetic Law was abandoned, and its fall freed scientists to appreciate the full range of embryonic changes that evolution can produce — an appreciation that has yielded spectacular results in recent years as scientists have discovered some of the specific genes that control development. |
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| Wallace's Oriental regionThis map from Wallace's 1876 book shows his Oriental biogeographic region, broken into four subregions (outlined in red). "Wallace's Line" is indicated by the arrow. Click for an enlargement. | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif |

Wallace pushed the study of biogeography to grander scales than Darwin. As he traveled through Indonesia, for example, he was struck by the sharp distinction between the northwestern part of the [archipelago](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=archipelago) and the southeastern, despite their similar climate and terrain. Sumatra and Java were ecologically more like the Asian mainland, while New Guinea was more like Australia. He traced a remarkably clear boundary that snaked among the islands, which later became known as "Wallace's Line." He later recognized six great biogeographical regions on Earth, and Wallace's Line divided the Oriental and the Australian regions.

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| Alfred Wegener | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif |

Plate tectonicsThe biogeographic regions of the world that Wallace recognized roughly coincide with the continents themselves. But in the twentieth century, scientists have recognized that biogeography has been far more dynamic over the course of life's history. In 1915 the German geologist Alfred Wegener (left) was struck by the fact that identical fossil plants and animals had been discovered on opposite sides of the Atlantic. Since the ocean was too far for them to have traversed on their own, Wegener proposed that the continents had once been connected. Only in the 1960s, as scientists carefully mapped the ocean floor, were they able to demonstrate the mechanism that made continental drift possible — plate tectonics.

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| Fossils common to the southern continents |
| http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif |
| Wegener found that the distributions of fossils of several organisms supported his theory that the continents were once joined together. |

Biogeographers now recognize that as continents collide, their species can mingle, and when the continents separate, they take their new species with them. Africa, South America, Australia, and New Zealand, for example, were all once joined into a supercontinent called Gondwanaland. The continents split off one by one, first Africa, then New Zealand, and then finally Australia and South America. The evolutionary tree of some groups of species — such as tiny insects known as midges — show the same pattern. South American and Australian midges, for example, are more closely related to one another than they are to New Zealand species, and the midges of all three land masses are more closely related to one another than they are to African species. In other words, an insect that may live only a few weeks can tell biogeographers about the wanderings of continents tens of millions of years ago.

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| tectonic plates |
| The Earth's crust has been found to be composed of several distinct plates. |

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Fossil Hominids, Human Evolution: Thomas Huxley & Eugene Dubois

When [Charles Darwin](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_14) wrote the *Origin of Species*, he had to wonder about how humans came to be. Humans had hereditary variation in every generation, and some individuals had more children than others — the key ingredients for [natural selection](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=natural+selection). But he chose not to write about humans in his first book about evolution, in large part out of strategy. In 1857, two years before Darwin published the *Origin of Species*, [Wallace](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_16) asked him in a letter if he would discuss the origin of mankind in the book. Darwin replied, "I think I shall avoid the whole subject, as so surrounded with prejudices, though I fully admit that it is the highest and most interesting problem for the naturalist."

But Darwin also knew that he had no fossil record to use to develop a hypothesis about human evolution. Over the years, naturalists had uncovered a few stone tools lying alongside the fossils of extinct mammals. But even in the 1800s, these relics were considered to be only a few thousand years old, and to have been made by lost tribes of savages.

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| http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | Neandertal and modern human skulls  |

First human fossils discovered
Even when the first part of a fossil human came to light in 1857, naturalists had a hard time recognizing it for what it truly was. German miners working at the Feldhofer Grotto in the Neander valley dug up a skullcap. It looked somewhat human, but it was remarkably thick and sported a massive brow ridge. Did it belong to an ancient individual from a human-like species now extinct? Or was Neanderthal man just an extreme member of *Homo sapiens*? One of the German naturalists who described the skull for the first time, Herman Schaaffhausen, was convinced of the latter. He ignored evidence that the skull had been found alongside extinct cave bears and mammoths, and claimed that it was some recent barbarian, perhaps a member of one of the wild tribes mentioned by Roman historians.

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| Thomas Huxley | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif |

Shortly after Darwin published the *Origin of Species*, his great champion Thomas Huxley (right) considered the skull from the Neander valley. Huxley shared some of the Euro-centric notions of his time. Based on their skulls, it was thought that Europeans had the best-developed brains, compared to the Australian aborigines with skulls having relatively low profiles and thicker brows. This view led Huxley to consider Neanderthals as occupying a slightly lower position within *Homo sapiens*.

Darwin publishes on human origins
Amid these ambiguous developments, Darwin decided to say something about human origins. In 1871 he published *The Descent of Man and Selection in Relation to Sex*, in which he argued that all of the known evidence was consistent with humans having evolved from a common ancestor shared with apes. He speculated that Africa was their place of origin and that human ancestors had gradually taken on their current form since then. He suggested that natural selection was not the only evolutionary pressure at work. Women might have preferred different traits in men, what Darwin called [sexual selection](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=sexual+selection), and this might have given rise to differences between the races. Darwin's ideas did not persuade his old correspondent, Alfred Russel Wallace. Wallace decided that our oversized brains were far more powerful than necessary — we could easily survive with minds slightly more advanced than an ape's. The creation of humans must, he concluded, be the work of divine intervention.

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| Eugene Dubois | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif |

More human fossils discovered
Fossils would be crucial to resolving this debate, but they were slow in coming. It was not until 1886 that Neanderthal fossils were discovered for a second time — and this time, they included the jaw and other parts of the skeleton. Found in Spy, Belgium, these clearly came from ancient rocks, demonstrating that Neanderthals were not some barbarian tribe that lived a few centuries ago. The next year, Eugene Dubois (left), a young anatomist from Holland traveled to Indonesia in the hopes of finding fossils of early man. Since orangutans lived there, and since Dubois managed to secure a job as a medical officer in the Royal Dutch East Indies Army, it seemed like a good place for him to go prospecting. After four years of struggles, he hit pay dirt when he dug a pit in the side of the Solo River in eastern Java. He found fossil remains of something not quite human, but not quite ape. It stood upright, but its brain was far too small to qualify as human. It became known as *Pithecanthropus erectus*, meaning "upright ape-man."



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| http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | Homo erectus skull |
| The *Homo erectus* skullcap discovered by Dubois. |

Fossil evidence and the acceptance of human evolution
Dubois came back to Europe in 1895 to champion his discovery. He met with some stiff opposition from skeptics. Some wondered whether the ape-like skull and the human-like femur came from the same skeleton. Others thought the skull was similar to Neanderthals. Dubois became embittered by the debate over his bones and hid the fossils from other scientists. But in time, as more fossils were uncovered in Asia, scientists came to recognize that Dubois had indeed found the first representative of the ancient species, *Homo erectus*.

The twentieth century brought a great many more fossils of humans and [hominids](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=hominid). Today twenty hominid species have been identified, the oldest of which date back six million years. They point to an African origin, as Darwin had proposed. Hominid evolution was sometimes pictured as a single line of descent and a steady progression from primitive forms to more advanced forms. The fossils suggested otherwise. Instead, hominid evolution produced a dense thicket of branches, with several species co-existing at any given time except for the last 30,000 years or so. Added to this wealth of data is the knowledge gathered from comparisons of [DNA](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=DNA) from humans, apes, and even Neanderthals. While many questions remain to be answered about human evolution, scientists have a growing treasury of evidence at their disposal.

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| Human tree | Left: One possible model of the somewhat bushy path of human evolution. The letters correspond to the following species:A-*Ardipithecus ramidus*B-*Australopithecus anamensis*C-*Australopithecus afarensis*D-*Australopithecus africanus*E-*Paranthropus aethiopicus*F-*Paranthropus robustus*G-*Paranthropus boisei*H-*Australopithecus garhi*I-*Homo rudolfensis*J-*Homo habilus*K-*Homo ergaster*L-*Homo erectus*M-*Homo heidelbergensis*N-*Homo neanderthalensis*O-*Homo sapiens* |

Random Mutations and Evolutionary Change: Ronald Fisher, JBS Haldane, & Sewall Wright

For 70 years after the publication of the *Origin of Species*, it seemed as if [Lamarck](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_09)'s shadow would loom forever over Darwin. On the one hand, most biologists came to the reality of evolution — that living species shared a common ancestry and had been transformed over time. But [natural selection](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=natural+selection) — the engine of evolution, according to Darwin — remained controversial. Many biologists argued that there must be some built-in "direction" to the variation that arose in each generation, helping to push each lineage towards its current state.

Many of these first geneticists who rediscovered [Mendel](http://evolution.berkeley.edu/evolibrary/article/0_0_0/history_13)'s insights around 1900 also opposed natural selection. After all, Darwin had talked of natural selection gradually altering a species by working on tiny variations. But the Mendelists found major differences between traits encoded by [alleles](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=allele). A pea was smooth or wrinkled, and nothing in between. In order to jump from one allele to another, evolution must make giant jumps—an idea that seemed to clash with Darwin.

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| Ronald Fisher | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif |

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| http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif | JBS Haldane |

Natural selection in a Mendelian world
But in the 1920s geneticists began to recognize that natural selection could indeed act on [genes](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=gene). For one thing, it became clear that any given trait was usually the product of many genes rather than a single one. A [mutation](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=mutation) to any one of the genes involved could create small changes to the trait rather than some drastic transformation. Just as importantly, several scientists — foremost among them Ronald Fisher (above left), JBS Haldane (above right), and Sewall Wright (below left) — showed how natural selection could operate in a Mendelian world. They carried out breeding experiments like previous geneticists, but they also did something new: they built sophisticated mathematical models of evolution.

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| Sewall Wright | http://evolution.berkeley.edu/evolibrary/images/dot_clear.gif |

Small, not drastic, changesKnown as "population genetics," their approach revealed how mutations arise and, if they are favored by natural selection, can spread through a population. Even a slight advantage can let an allele spread rapidly through a group of animals or plants and drive other forms extinct. Evolution, these population geneticists argued, is carried out mainly by small mutations, since drastic mutations would almost always be harmful rather than helpful. Wright introduced the most compelling metaphor in population genetics, known as the "adaptive landscape" (see figure, below). You can imagine the varying [fitness](http://evolution.berkeley.edu/evolibrary/glossary/glossary_popup.php?word=fitness) of different combinations of genes as a hilly landscape, in which the valleys represent less-fit combinations of genes and the peaks represent the fitter ones. Natural selection tends to move the populations towards the peaks of the hills. But since the environment is always changing, the peaks shift, and the populations follow after them in a never-ending evolutionary journey. |



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|  | Map of malaria distributionMap of sickle-cell anemia distribution  |  | Top: Distribution of malaria in southern Europe, southwest Asia, and Africa around 1920 (green), prior to mosquito eradication programs. Bottom: Distribution of the sickle-cell allele within the same area. The darker the blue,the greater the percentage of people carrying the allele. Note the correlation between these maps. |

Natural selection in the wild
Population genetics became one of the key elements of what would be called the Modern Synthesis. It showed that natural selection could produce evolutionary change without the help of imaginary Lamarckian forces. Scientists have used the mathematical tools developed by Fisher, Wright, and Haldane to measure evolutionary change in the wild with exquisite precision. Their insights have even allowed medical researchers to decipher the puzzle of some hereditary diseases. Sickle-cell anemia, for example, is caused when children inherit two defective copies of a gene involved in making hemoglobin. But a single copy of this allele can give some protection against malaria (see figures, right). Natural selection finds a balance between the reproductive disadvantage of being born with two copies of the allele and the advantage of having one. Genetic disorders such as sickle-cell anemia are actually the agonizing byproduct of natural selection acting on our ancestors.